THE BASES OF ANGIOSPERM PHYLOGENY: EMBRYOLOGY

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ABSTRACT

Many of the embryological characteristics that may be useful, when employed judiciously and in conjunction with other characters, in arriving at taxonomic conclusions are listed. Several characteristics that show a non-random distribution between families of the Magnoliatae and those of the Liliatae are discussed. Features which are more predominant in the monocotyledons than dicotyledons are: monocotyledonous type of development of the anther wall; amoeboid tapetum; successive cytokinesis of the microspore mother cells to form isobilateral tetrads; helobial endosperm development; and a single cotyledon in the mature embryo. In contrast, those characteristics that are more prevalent among dicot families than monocot families include: basic and dicotyledonous patterns of anther wall formation; simultaneous cytokinesis of microspore mother cells with the formation of tetrahedral tetrads; hemitropous, amphitropous, or circinotropous ovules; ovules with a single integument; an endothelium; *Oenothera*, *Penaea*, *Peperomia*, *Plumbago*, or *Plumbagella* types of megagametophyte development; cellular endosperm; and two cotyledons in the mature embryo. In spite of these differences, those characteristics that are most common—occurring in at least 70%, and usually more, of all angiosperms—are evenly distributed between the two classes and afford a strong embryological unity to the angiosperms. These widespread characters include: four microsporangia per anther; differentiated endothecium; two-celled pollen grains; bitegmic anatropous ovules; *Polygonum* type of megagametophyte development; and nuclear endosperm. Within the two classes distribution of the various characters is not always proportional among the several subclasses and superorders; for example, a unitegmic, tenuinucellate ovule with an endothelium, cellular endosperm with haustoria and Solanad embryogeny predominates in the Ericanae and Asteridae; or helobial endosperm is a distinctive feature of the Alismidae. On the whole, embryological characteristics are remarkably constant at the family level. In those families where variation does occur, genera are usually constant, although a few notable examples of intrageneric, and even intraspecific, variation do exist, as for example, in patterns of megagametophyte development. In addition to the taxonomic usefulness of the grosser aspects of embryology—the major categories of structure or development—some evidence is presented suggesting that variation in details within a single category, such as size, shape, and cellular characteristics of the developing and mature megagametophyte, may be helpful in determining relationships within families, genera, or species.

Since the time of the nineteenth century landmarks in embryological knowledge and the men who made the observations (Amici's discovery of the pollen tube, Hofmeister's recognition of the general structure of the mature megagametophyte and meiosis in microspore mother cells, Strasburger's working out of stages in megagametophyte development and observation of fertilization, and finally the independent recognition that fertilization was double by Nawaschin and Guignard [see Maheshwari, 1950]), many descriptions of various aspects of sexual reproduction (embryology in the broad sense) in a wide variety of angiosperm plants have been published by a host of botanists. During the early part of this century some use was made of embryological characteristics for systematic purposes, for example, Samuelsson's (1913) treatment of the Ericaceae, but it was only with the publication of Schnarf's (1931) *Vergleichende Embryologie der Angiospermen* that impetus was given to this type of synthesis of the accumulating embryological information. Since that time a number of papers, review articles, or books have

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appeared treating one or more embryological characteristics on a comparative basis, frequently relating the observations to one or more taxonomic schemes. This paper is yet another brief attempt in this direction. Throughout, the term "embryology" will be used in the broad sense and is conceived of as incorporating anther, ovule, micro- and megasporogenesis, development of gametophytes, fertilization, and growth of endosperm, embryo, and seed coats.

TECHNIQUES

The early observers, such as Hofmeister, worked almost entirely with fresh and hand-sectioned materials. With the development of paraffin embedding and microtome sectioning, these techniques largely replaced the earlier ones, and the bulk of the observations reported in the literature have been based on thin, stained, serial sections of flowers, ovaries, or ovules. In addition, squashes and smears of anthers have been extensively used, particularly for stages in meiosis and pollen development. In some cases where the megagametophyte, endosperm, or embryo develops highly irregular haustoria which ramify through ovular and/or placental tissues, there has been, during the last 20 years, a return to use of fresh material. Dissections of ovules, combined with microtome sections, have clarified the development and organization of such haustoria (see Chopra & Agarwal, 1958). Dissections have also been used, along with microtome sections, in elucidating embryo development.

The processes of paraffin embedding, microtome sectioning, and staining are relatively tedious. When this is coupled with the facts that such sections are in one plane only, that anthers and ovules may be oriented in a variety of ways even in a single flower (so that "good" sections are often rare and structure must be reconstructed from serial sections), and that for most embryological determinations a closely graded series of developmental stages is needed, it is easy to understand why the number of species for which essentially complete embryological information is available is almost infinitesimal as compared to the total number of angiosperm species. A larger number of species is known with respect to one or a few characteristics, but the total is still very small when compared to the number of angiosperms recognized. This, of course, means that all generalizations based on present knowledge are subject to rejection, modification, or strengthening, as the body of available information increases.

In an attempt to circumvent the tedious aspects of microtome sectioning and the resultant slow accumulation of data for comparative purposes, Herr (1971) has recently developed a technique for clearing and squashing ovules to obtain information on megasporogenesis and megagametogenesis more rapidly. One example of the use of this technique is Smith's (1973) recent study of five species of *Cornus*.

During the past several years embryological materials, particularly pollen, mature megagametophyte, and early embryo, have been prepared for observation with the electron microscope or studied histochemically. These processes are probably even more time-consuming and, to date, with the possible exception of pollen, information is inadequate for use on a broad comparative basis.

MAJOR REFERENCE WORKS

During the early part of this century, embryological data accumulated rather rapidly and most of the major differences in developmental patterns and structure were recognized. The first text to be based on this extensive information was Schnarf's (1929) *Embryologie der Angiospermen*; this was followed by Maheshwari's (1950) *Introduction to the Embryology of Angiosperms*, and a fair-sized portion of Eames' (1961) *Morphology of the Angiosperms* is devoted to embryology. Maheshwari's text was updated by a series of papers on different embryological topics published, under Maheshwari's (1963b) editorship, as chapters in *Recent Advances in the Embryology of Angiosperms.* The most recent contribution is *The Embryology of Angiosperms* by Bhojwani & Bhatnagar (1974). These books incorporate definitions of terms, descriptions of various developmental patterns and mature structures in all aspects of embryology with their variations, some discussion of possible phylogeny within characters and taxonomic applications of the observed variability, and brief presentations of the physiological and experimental aspects of embryology (which have been less extensively studied than the descriptive ones). Wulff & Maheshwari's (1938) and Maheshwari's (1949) review articles on the male gametophyte of angiosperms are examples of broad treatments of a particular embryological character and there are others of a similar type.

There have been two major attempts to bring together all embryological data on a comparative basis: Schnarf's (1931) book and Davis's (1966) *Systematic Embryology of the Angiosperms.* A Seminar on Comparative Embryology of Angiosperms was held at the University of Delhi in 1967 and, under the editorship of Johri et al. (1967), synopses of the characteristics of 130 families were published. These constitute the major references which deal with all aspects, but books or review articles which sum up individual embryological characteristics on a family basis also occur: Johansen (1950) dealt with embryogeny, Wunderlich (1954, 1959) with tapetum and endosperm, Swamy & Parameswaran (1963) with helobial endosperm, Swamy & Krishnamurthy (1970) with the endothelium in monocotyledons, and Brewbaker (1967) with bi- and trinucleate pollen grains. Souèges, and his students, studied embryogeny in a wide range of species and proposed a classification scheme for embryo development (see Crété, 1963, where much of this work is summarized). A simplification of this classification has been proposed by Mestre (1967) to allow incorporation of species omitted from Souèges's scheme. A third way of classifying embryogeny (Yamazaki, 1974) purports to be more "natural" than those of Johansen and Souèges. Other papers, still more restricted in scope (for example, ones discussing the bisporic or tetrasporic megagametophytes), have been published, but these will not be cited.

Several authors have attempted to show how embryological data may be used for taxonomic purposes, frequently by citing particular genera, tribes, families, or even orders (the examples are in part repetitious from one paper to another): for example, Poddubnaja-Arnoldi (1928), Schnarf (1933), Mauritzon (1939), Maheshwari (1950: chap. 11, 1956, 1961, 1963a), Kapil (1962), Subramanyam (1962), Johri (1963, 1967), Crété (1964), and Bhojwani & Bhatnagar (1974: chap. 13). There have also been listings of those embryological characteristics that may be useful taxonomically, as for example, those by Schnarf (1933), Maheshwari (1950, 1963a), Cave (1962), Davis (1966), and Bhojwani & Bhatnagar (1974). Just (1946) recommended the use of embryological formulas in the diagnoses of angiosperm taxa much as floral formulas are used.

EMBRYOLOGICAL CHARACTERISTICS WHICH MAY BE USEFUL FOR TAXONOMIC PURPOSES

The following list of characters has been compiled in large part from those previously published lists (see above) and makes no claim to being exhaustive, but the more significant features have been included. It is unlikely that all characteristics are of equal importance. For descriptions, diagrams, drawings, etc. of the various characteristics the reader referred particularly to Maheshwari (1963a, 1963b).

Anther and pollen
- Number of microsporangia.
- Type of wall development: basic, dicotyledonous, monocotyledonous, reduced.
- Endothecium: differentiated or not; number of layers.
- Tapetum: glandular or amoeboid; number of nuclei per cell and whether polyploid or not.
- Delimitation of microspores: simultaneous or successive; by furrowing or cell-plate formation.
- Type of tetrad: tetrahedral, decussate, isobilateral, linear, T, rhomboidal.
- Microgametophyte or pollen grain: place of formation of generative cell; number of cells at time of shedding; single or in a cluster, and size of cluster; external morphology such as apertures, exine characteristics, etc. (The latter will be omitted from consideration here and left for the palynologists.)

Ovule
- Type: anatropous, orthotropous, campylotropous, hemi(ana)tropous, amphitropous, circinotropous.
- Integument(s): one or two; micropyle formed by inner, outer, or both integuments, and if both, straight or zigzag.
- Vascular tissue: present or absent; if present, where?
- Adjuncts to ovule (pre- or post-fertilization): aril, arillode, caruncle, obturator, etc.
- Nucellus: crassi-, pseudocrassi-, or tenuinucellate; nucellar beak? persistent during development? special areas—hypostase, epistase, postament, etc.
- Endothelium: present or absent; when present, extent of coverage of megagametophyte.

Megasporogenesis and megagametogenesis
- Archesporium: number of cells? divides to form parietal tissue or not.
- Type of tetrad: linear, T, ⊥, isobilateral, tetrahedral, coenocytic.
- Position of functional megaspore.
- Pattern of megasporogenesis and megagametophyte development: *Polygonum*,

Oenothera, *Allium*, *Peperomia*, *Penaea*, *Drusa*, *Fritillaria*, *Plumbagella*, *Plumbago*, or *Adoxa* type.

Mature megagametophyte: shape; characteristics of synergids and antipodal cells; position and fusion of polar nuclei; type of food reserve, if any.

Haustoria: present or absent; origin and extent.

Fertilization and post-fertilization development

Path of pollen tube: porogamous, chalazogamous, mesogamous.

Endosperm: type of development—nuclear, helobial, cellular and if cellular, orientation of first walls; haustoria—present or absent, origin and extent; persistence in seed; food reserve; ruminate?

Embryogeny: type of development (Johansen, 1950)—Asterad, Onagrad, Chenopodiad, Solanad, Caryophyllad, Piperad; suspensor haustoria present or absent, origin and extent; mature embryo.

Persistence of nucellar tissue in seed.

Source and structure of seed coat.

Apomixis, polyembryony, etc.

COMPARATIVE EMBRYOLOGY IN THE ANGIOSPERMS

The facts on which the following comparisons are made are taken primarily from Davis's (1966) book, supplemented by the published synopses from the seminar on comparative embryology at Delhi (Johri et al., 1967) and over 100 individual papers published from 1967 to early 1973.[2] No attempt was made to obtain complete coverage of the pertinent literature for the past 6 to 7 years; only a few journals were checked for embryological articles.

Certain difficulties arise with using Davis's book as the major source of information. There is only indirect evidence of the number of genera and species that have been described in any one family and on which the generalizations are based: the number of papers cited, and, when a family is variable, the number of representatives which may be named. In the seminar synopses no citations are given, so even this type of evidence is missing. Thus, in some families the facts may be based on a single genus or species, while in other families the number of species described has been very much larger. Another and similar problem occurs when a family is described as having two or more variants of a particular characteristic (for example, tetrahedral, decussate, and isobilateral tetrads of microspores or "anatropous to campylotropous" ovules). Often no indication of the relative frequency of the variants is given. Another difficulty is that certain of the characteristics listed as possibly of taxonomic usefulness are not included at all or are mentioned for only a few families. Information may have been lacking in the original papers summarized and/or, faced with the immensity of the task confronting her in compiling the embryological data, Davis may have decided to omit some aspects as probably being of less significance. Whatever the deficiencies of Davis's book, and they are minor compared to the advantages, the task set me for this symposium would have been impossible without her extensive compilation of information.

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[2] These papers are not cited, but a mimeographed list may be obtained from the author on request.

Before starting the factual comparisons, it is probably well to reemphasize that the number of angiosperm species known embryologically, in whole or in part, is very small as compared to the total number of species. Even in one of the more thoroughly studied families, the Asteraceae, Davis (1966) pointed out that, although her bibliography contained over 300 references pertaining to the family, these papers dealt with species in only 15% of the genera and most of the publications were concerned with only one aspect of embryology.

Certain precautions also should be mentioned. In any attempt to arrive at a natural or phylogenetic classification of angiosperms, a single characteristic or single category of characteristics, such as embryology, should not be the sole basis for determining the relationships of a taxon. Although in the following discussion embryological characteristics only are considered, they should be used in conjunction with data from other fields of knowledge, such as those represented in this symposium, in arriving at conclusions. As with other areas, it seems evident that evolution has not proceeded at the same pace in all embryological characteristics, and species may exhibit what is usually considered a basic or primitive variant of a particular characteristic, such as a bitegmic, crassinucellate ovule, along with a derived variant of another, such as a tetrasporic pattern of megagametophyte development. Some variants will have arisen more than once and similarities among species may be the result of parallel or convergent evolution rather than direct relationship. In addition, as pointed out by Davis (1966: 6), "characters are not absolute and their value must be reassessed for each taxon. . . . In other words, the nature of taxonomic characters varies with the taxon."

For several of the embryological characteristics listed earlier, a particular variant is very much more prevalent among angiosperms than the other variants of the same characteristic. There is fairly general agreement that, at least for some of these characteristics, each of the predominant variants represents the basic or more primitive aspect and the other variants are derived. The following constitute these more "primitive" expressions of embryological characters: four microsporangia per anther; two-celled pollen; anatropous, bitegmic, crassinucellate ovule with a multiple archesporium and *Polygonum* type of megagametophyte development; chalazal spore functional; and endothelium absent. There is much less consensus about the phylogenetic status of other characteristics such as the different types of microspore tetrad formation, endosperm development, and embryogeny.

DISTINGUISHING MAGNOLIATAE AND LILIATAE

The distinction between the Magnoliatae and Liliatae is not marked by obvious differences in embryology. Davis (1966: 7) pointed out this embryological unity of the two angiosperm classes in this way: "Hutchinson (1959) recognizes 411 families, of which 342 (83.2%) are dicotyledonous. At the outset, then, there is a dicotyledon to monocotyledon ratio of 5 to 1, so that any character which occurs in five times as many dicotyledonous as compared to monocotyledonous families has an equal frequency in the two groups. . . . it is remarkable that this ratio is almost always so closely approximated. The fact that this does occur, however, supports the opinion of various authors that there is no embryological distinction between dicotyledons and monocotyledons."

The one most consistent embryological criterion for distinguishing between the Magnoliatae and Liliatae (taxon names throughout are those of Cronquist, 1968 and/or Takhtajan, 1969) is that which led to the original names of the two classes: two or one cotyledons in the mature embryo. This distinction is by no means sharp, however (see Eames, 1961). There are a number of dicotyledons with more than two cotyledons: three occur in most seeds of *Degeneria* as well as in others of the Magnoliales; three commonly are found in *Acer* and *Juglans*; or more than three occur in certain species of *Persoonia* and *Loranthus.* Pseudomonocotyledony occurs more commonly than polycotyledony: either the two cotyledons are of unequal size or one has been lost so that the embryo has a single cotyledon. In such genera as *Trapa* and *Mammillaria* one cotyledon is smaller than the other, while in *Cyclamen* one is well-developed, the other only a small vestige. Two species of *Corydalis* have one normal cotyledon but the second is only a bump opposite it. One species of *Pinguicula* has one normal cotyledon and a second one which stops developing at various stages; two different species have a single cotyledon. *Ranunculus ficaria* is perhaps the best known example of a dicot with a single cotyledon; in this species two cotyledons are initiated and while one most commonly aborts, occasionally both develop. Suppression of one of the two cotyledons is more prevalent in the Apiaceae than any other family: in eight genera the species have one cotyledon while in two other genera some species have two, some one. Aberrant embryos are less common in the monocotyledons, but some genera of the Dioscoreaceae and Commelinaceae have a second cotyledon present in reduced form. *Arum, Arisaema, Trillium,* and *Paris* have been interpreted as having two cotyledons, one foliaceous (often called the first leaf) and the second a well-developed absorptive organ. Both arise at the same level of the hypocotyl, and their vascular supplies are equal and opposite.

Some other characteristics which are more prevalent in the Magnoliatae or in the Liliatae will be discussed briefly.

1. Type of Anther Wall Formation.—The names given by Davis (1966) to two of the four patterns of anther wall development she recognized, dicotyledonous and monocotyledonous, suggest a distinction between the two classes, which, at the present state of our knowledge, does exist. It should be pointed out, however, that information is available for only about 21% of the families and is based, in most cases, only on one or a few species in a family. So far, the basic type has been reported only in dicotyledonous families and, with one possible exception, the same is true of the dicotyledonous type. While the monocotyledonous type is listed as the only type of development in 15 dicot families and as occurring in at least one genus of 7 others, very few monocots are reported to show any other pattern of wall formation.

2. Tapetum.—The innermost anther wall layer, supplemented by cells of the connective in contact with the sporogenous tissue, constitutes the tapetum. (Some reports describe the tapetum of certain species as being derived from sporogenous rather than wall plus connective tissue—see Steffen & Landmann, 1958.) Two basic types are generally recognized—glandular or secretory (which remains cellular and degenerates in situ) and amoeboid (in which the walls break down and the cytoplasm and nuclei migrate among the microspore mother cells)—although Carniel (1963) and Steffen & Landmann (1958) also describe a false periplasmodial tapetum. Those families which show a glandular tapetum exclusively (several families are reported to have both) are 87% dicotyledonous. This is only slightly higher than the normal ratio. An amoeboid tapetum is less common, but 63% of the families in which it is the only type recorded are monocotyledonous; it is the only type found in the Alismidae. The dicot families showing an amoeboid tapetum are scattered from the Magnoliidae to the Asteridae, with more occurring in the superorder Lamianae than elsewhere. Thus, an amoeboid tapetum shows a definite tendency to occur in the monocots rather than the dicots.

3. *Cytokinesis and Microspore Tetrad.*—The first meiotic division of the microspore mother cell may be accompanied by formation of a wall separating the two nuclei; wall formation again occurs after the second division, and cytokinesis is described as successive. In contrast, wall formation may be delayed until after meiosis II has been completed at which time walls separating the four spores form simultaneously. Again, a few families, both monocot and dicot, are reported to show both patterns of cytokinesis, but the majority are characterized by one or the other. Better than 95% of the families showing simultaneous wall formation are dicots while approximately 92% of those with successive wall formation are monocots. Most of the exceptions occur among the Magnoliidae and Asteridae in the dicots, and the Liliidae among the monocots. Maheshwari (1950) stated that, with a few exceptions, simultaneous cytokinesis is accomplished by furrowing from the periphery and successive cytokinesis by cell-plate formation starting in the center; this cannot be corroborated since the method of division is given for very few families by Davis (1966). Maheshwari (1949) further stated that in dicotyledons the tetrad is usually tetrahedral while in the monocots it is isobilateral. This would suggest a correlation of simultaneous cytokinesis with tetrahedral tetrads and of successive cytokinesis with isobilateral tetrads. Since Davis lists two or more tetrad types for the majority of families, with no indication of the relative frequency of the different forms, this statement and correlation are difficult to check. Those families for which a single type is listed (only 73 out of 214) fit well: 57 dicots to 2 monocots with tetrahedral tetrads, and 2 dicots to 12 monocots with isobilateral tetrads. In addition there is only one family reported to have simultaneous cytokinesis plus only isobilateral tetrads.

4. *Number of Cells in Shedding Pollen.*—Two-celled pollen as a family characteristic has close to a normal distribution between monocots and dicots, but three-celled pollen is somewhat more prevalent among the Liliatae with 37% of the 47 families showing only three-celled grains being monocotyledonous.

5. *Ovule Type.*—Of 234 families characterized by a single type of ovule, 197, proportionately distributed among the two angiosperm classes, have an anatropous ovule. Those families having only hemitropous (10) or amphitropous (4) ovules are all dicotyledonous and a circinotropous ovule has not been reported

from any monocot family. Orthotropous ovules are the only ones reported for 18 families, 13 of which are dicots and 5 monocots, while of 5 families having campylotropous ovules 3 are dicots and 2 monocots. Thus hemitropous, amphitropous, and circinotropous ovules might be considered basically dicotyledonous. Hemitropous ovules do occur in certain monocot families, however, in conjunction with other ovular types, primarily anatropous and orthotropous. The only families in which the ovule is so reduced as to be essentially nonexistent as a distinct ovule are dicotyledonous.

6. *Integuments.*—The reduced "ovules" just referred to and those in several genera of another dicot family are ategmic. In 92 dicot but no monocot families the ovules are exclusively unitegmic. Unitegmic ovules do occur among monocots, however, along with bitegmic ones in two families of the Liliidae. Of 210 families in which only bitegmic ovules are found, 59, or close to 30%, are monocotyledonous. Thus, unitegmic and ategmic ovules are a feature found almost entirely in the Magnoliatae. When there are two integuments, the micropyle may be formed by the outer alone, the inner alone, or by both. Families characterized by a micropyle formed by the inner integument are a little more common than those in which it is formed by both (92 to 75) while only two dicot families, both in the Dilleniidae, and not any monocot genera, have micropyles formed by the outer integument alone. About one-third of the families with an inner integument micropyle are monocotyledonous and only about one-sixth of the families with both integuments involved are among the Liliatae.

7. *Endothelium.*—The endothelium is a layer (occasionally more than one) of narrow, radially elongated, more highly cytoplasmic cells which differentiates, concurrently with or subsequent to the degeneration of the nucellus, from all or part of the innermost layer of the integument that is in contact with the megagametophyte. Swamy & Krishnamurthy (1970) discussed the one or more species in 7 different monocot families which had been reported to have an endothelium. They reached the conclusion that in all these cases the layer in question should be interpreted as a temporary stage in development and not as a true endothelium. Davis (1966) apparently largely agrees with this interpretation because she lists only 2 families of monocots as exhibiting an endothelium in contrast to 67 dicot families. Swamy and Krishnamurthy further stated that the families of Magnoliatae with an endothelium are of two types: 18 have crassinucellate, bitegmic ovules later developing nuclear endosperm, while the majority (about 50) possess tenuinucellate, unitegmic ovules and later produce cellular endosperm. They indicated that they would discuss the 18 families in a later publication, but the implication was that these, like the monocots, do not produce a typical endothelium. If their interpretation can be accepted, endothelial development is limited to a comparatively small group of relatively advanced dicotyledonous families. Even if the interpretation is not accepted, an endothelium is primarily a feature of ovules of dicot families in the Dilleniidae, Rosidae, and Asteridae.

8. *Ovule Archesporium.*—The hypodermal cell (or cells) at the tip of the young nucellus which gives rise to the megaspore mother cell(s) constitutes the archesporium. There may be one cell, two, or several. While a unicellular archesporium is proportionately distributed among the families of the two angio-

sperm classes, a multicellular condition is not: it is regular in 43 and frequent in 23 dicot families in contrast to regular in 2 and occasional in 1 monocot families.

9. Megagametophyte Development.—The patterns of development from megaspore mother cell to mature megagametophyte are based on the number of spores that take part in the development, the number of mitotic divisions after the two meiotic ones, the total number of nuclei at the completion of divisions, and the cellular organization of the mature gametophyte. The *Polygonum* type (monosporic; 3 mitoses; 8 nuclei; and 2 synergids, 1 egg, 2 polar nuclei, and 3 antipodal cells) is by far the most common, occurring exclusively in close to 80% of the families and distributed equally between the Liliatae and Magnoliatae. The other patterns of development are much less frequent and only in 11 families, 8 of them dicot, is one of them the only developmental type exhibited. Certain of these other types, namely *Oenothera* (monosporic; 2 mitoses; 4 nuclei; and 2 synergids, 1 egg, and 1 polar nucleus), *Penaea* (tetrasporic; 2 mitoses; 16 nuclei; 2 synergids, 1 egg, 4 polar nuclei, and 3 groups of 3 "antipodals"), *Peperomia* (tetrasporic; 2 mitoses; 16 nuclei; and 2(1) synergids, 1 egg, 7(8) polar nuclei, and 6 scattered antipodals), *Plumbago* (tetrasporic; 1 mitosis; 8 nuclei; and 1 egg, 4 polar nuclei, and 3 widely separated "antipodal" cells), and *Plumbagella* (tetrasporic; 1 mitosis; 4 nuclei; and 1 egg ($1n$), 2 polar nuclei ($1n$ and $3n$), and 1 antipodal cell ($3n$)), have to date not been reported in any monocotyledonous species. The other four types, *Allium* (bisporic; 2 mitoses; 8 nuclei; and 2 synergids, 1 egg, 2 polar nuclei, and 3 antipodal cells), *Drusa* (tetrasporic; 2 mitoses; 16 nuclei; and 2 synergids, 1 egg, 2 polar nuclei, and 11 antipodal cells), *Fritillaria* (tetrasporic; 2 mitoses; 8 nuclei; and 2 synergids ($1n$), 1 egg ($1n$), 2 polar nuclei ($1n$ and $3n$), and 3 antipodal cells ($3n$)), and *Adoxa* (tetrasporic; 1 mitosis; 8 nuclei; and 2 synergids, 1 egg, 2 polar nuclei, and 3 antipodal cells), occur in both classes, the *Allium* type being the more common in both.

10. Pollen Tube Entry.—In the vast majority of angiosperms the pollen tube enters the ovule porogamously, that is, via the micropyle. In five dicot families pollen tube penetration is chalazogamous; it enters the chalazal end of the ovule and follows a course along the lateral surface of the megagametophyte until it reaches the micropylar end where it enters the gametophyte itself in the usual fashion. One dicot family is mesogamous, with the pollen tube initially penetrating the ovule at some side point before making its way to the micropylar end of the gametophyte. No monocotyledonous genera have been reported to show either chalazogamy or mesogamy.

11. Endosperm.—Nuclear endosperm development results when division of the primary endosperm nucleus—the product of fertilization of the polar nuclei—and of subsequent nuclei is not followed by wall formation leading to a coenocytic condition. The number of free nuclei formed varies from relatively few to well in the hundreds before wall formation starts, but in most species, though not all, the endosperm does become cellular—usually completely but sometimes only in part. In direct contrast to the nuclear is the cellular type of endosperm development in which nuclear divisions are accompanied by wall formation (most commonly throughout development, but at least during the early stages) and the endosperm is cellular from the beginning, not just in later stages. In helobial endosperm development division of the primary endosperm nucleus is followed by wall formation, but the two cells formed are normally of very different sizes—the micropylar large and the chalazal small. Subsequent development in the micropylar chamber corresponds to the nuclear pattern—at first coenocytic, then becoming cellular. In the chalazal chamber the nucleus may remain undivided or undergo a few to several divisions, but the portion of the endosperm which it forms always remains much smaller than that formed by the micropylar chamber. Reports of helobial endosperm describe the chalazal chamber as being free nuclear in some families, cellular in others. Because of its small size it is quite possible that the chalazal chamber has been overlooked in some cases, or interpreted as a persistent antipodal cell, and since the behavior of the micropylar chamber is nuclear, endosperm development may have been mistakenly classed as nuclear in these cases. Of these patterns nuclear development occurs in the largest number of families, helobial in the fewest. Nuclear development shows a proportionate distribution between Liliatae and Magnoliatae, but cellular and helobial do not. Of 82 families showing only cellular endosperm, 80 are dicotyledonous and among 6 "mixed" monocot families only 1 is reported to have any species exhibiting cellular development. Helobial endosperm shows the opposite distribution: of 17 families in which the endosperm is exclusively helobial, 15 are monocotyledonous and of the 21 "mixed" dicot families only 6 are reported to show some species with helobial endosperm. Swamy & Parameswaran (1963) have reviewed the occurrence and characteristics of the helobial pattern of development. They discussed endosperm development in many dicot genera, particularly among 12 genera in the tribe Saxifraginae. They point out three distinguishing characteristics between helobial endosperm as it occurs in monocots and that reported in dicots. (a). In monocots division of the primary endosperm nucleus occurs close to the antipodal cells and the chalazal chamber is always much smaller than the micropylar, while in dicots the position of the division is variable and the chalazal chamber is not always smaller than the micropylar. (b). Initial divisions in the micropylar chamber are free-nuclear in both dicots and monocots but cell formation, if it occurs, takes place before the chalazal chamber becomes cellular in monocots and after it is cellular in dicots. (c). Any divisions that occur in the chalazal chamber are nuclear in monocots and cell formation, if it occurs at all, succeeds that in the micropylar chamber. In dicots cell formation in the chalazal chamber occurs at the first and subsequent divisions in a number of genera. In others, although the initial divisions are nuclear, cell formation in the chalazal chamber precedes that in the micropylar chamber. Swamy & Parameswaran (1963: 48) concluded that "the presumed cases of helobial endosperm in dicotyledons represent, in each case, a modified aberrant ontogeny of the general condition (cellular or nuclear) occurring in the respective families. Therefore, such ontogenies in the dicotyledons are totally removed ontogenetically and phylogenetically from the true helobial ontogeny of the monocotyledons." If one accepts their interpretation, the "true" helobial endosperm becomes even more a distinctive characteristic of the Liliatae. Micropylar, chalazal, and/or lateral portions of the endosperm may grow out to varying sizes and shapes and invade integument(s), funiculus, placenta, etc. where they apparently serve an haustorial function. Haustoria (ignoring variations in position and structure) may be associated with nuclear endosperm but are much more common with cellular endosperm, and the chalazal chamber of helobial endosperm is frequently haustorial. Because of the prevalence of haustoria in association with cellular endosperm and of this type of endosperm in dicots as compared to monocots, endosperm haustoria are more common in dicots. This difference in distribution of haustoria is offset to some extent by the greater frequency of helobial endosperm, and its associated chalazal haustorium, in monocots. Crété (1951) has enlarged on the distribution and phylogenetic interest of endosperm haustoria in angiosperms, particularly in the sympetalous dicotyledons. Eames (1961) stated that endosperm persists in the seed of more monocots than dicots, but data were not presented in Davis's (1966) summary of characteristics to allow confirmation of this statement.

12. Embryogeny.—The earlier two of the three systems of classification of embryo development—Johansen's (1950) and Souèges's (see Crété, 1963)—are based on the same criteria: first on the plane(s) of division during the first few cell generations and then on the relative contribution to the mature embryo of the individual cells of the proembryo, while in Yamazaki's (1974) classification emphasis is primarily on the latter aspect. Souèges's scheme is the more detailed of the three and a larger number of general types is recognized. To classify a particular species according to this scheme, a high degree of accuracy is needed in following the cell-by-cell development of the proembryo, more than is usually given in most descriptions. Johansen's system, while requiring careful observation particularly at certain critical stages, permits a classification as to type of development for most embryos described in the literature, and it is this system which Davis (1966) employed in her compilation. Yamazaki's key to embryogenic types had not been published at the time Davis was preparing her book, but I doubt that she would have used it in preference to Johansen's. Considering only the six basic types of development and none of the variations (which Johansen recognized within all but one type), embryogeny in 166 families follows a single pattern of development while in 105 two or more patterns are reported. Distribution between monocots and dicots is not the same for the several patterns: Piperad and Solanad types have not been reported in any monocot, not even in the "mixed" families, and most of the other types do not show the 5 dicot to 1 monocot segregation expected if distribution were proportionate between the two classes. The Chenopodiad type is characteristic of 5 dicot and 1 monocot families but the others diverge more or less from this: Onagrad type 40 to 4, Asterad type 41 to 10, and Caryophyllad type 12 to 13. The "mixed" families show a similar distribution of embryogenic types, except for the Caryophyllad type which has been reported to occur in at least one genus of 16 dicot families as compared to 3 monocot families.

Thus, if one looks carefully, it is possible to find uneven distribution between the Liliatae and Magnoliatae of several embryological characteristics, but this does not mean that it would be easy to classify an unknown species to one class or the other on the basis of embryology alone. In the characters that vary between the two, except for the number of cotyledons, the unevenness is expressed in one of two ways. (a). A shift occurs in the relative frequency of occurrence, by family, of that characteristic up or down from the approximate 5 to 1 ratio that would be expected if the characteristic were equally distributed among the families of the two classes (5 dicot families to 1 monocot family). When the shift in frequency of occurrence of a characteristic is toward the dicotyledons, there is an exaggeration of the difference in number of dicot and monocot families showing the character, but this may not be readily apparent without an overall comparison of the type just made. When the shift is in the opposite direction, toward the monocotyledons, the difference also is not readily apparent. Because of the considerably larger number of dicot families, even if the ratio shifts from 5:1 to 2:1, there will still be more dicot than monocot families exhibiting the characteristic. Examples of divergence from the expected frequency are seen in the distribution of tapetal types, bitegmic ovules, three-celled pollen grains, etc. (b). When the difference in distribution is much more clearly expressed, as when a particular characteristic occurs exclusively, or almost exclusively, in either the monocots or the dicots, that character almost always is one which occurs in a relatively small proportion of angiosperm families or genera. Some examples are certain of the types of megagametophyte development (*Penaea, Peperomia, Oenothera,* etc.), helobial endosperm, Piperad or Solanad embryogeny, and chalazogamous pollen tube penetration. The most common structures or patterns of development, such as *Polygonum* megagametophyte development, bitegmic anatropous ovule, nuclear endosperm, anthers with four microsporangia and a differentiated endothecium, are evenly distributed in the two classes resulting in the considerable embryological homogeneity that characterizes the angiosperms.

DISTINGUISHING HIGHER LEVEL TAXA WITHIN THE MAGNOLIATAE AND LILIATAE

Having seen to what use embryological characters can be put in attempting to distinguish between the two classes of angiosperms, the question remains as to whether such characteristics may be more or less useful as distinguishing features among taxa at various lower levels of the taxonomic hierarchy. Because there are so many embryological features which show variation and because this report makes no pretense at being an exhaustive survey of the subject, it has been necessary to select only some of these characters for discussion. Some aspects already considered with respect to dicots versus monocots will be omitted from further discussion; others will be touched on again but from another point of view.

The number of cells, often seen only as nuclei, in the pollen grains at the time they are shed from the anther may be two or three, as already pointed out. Distribution of families showing two-celled, three-celled, or both types of grains by subclass gives no clearcut distinctions, but families with two-celled grains or both two- and three-celled ones predominate in the Magnoliidae, Ranunculidae, Hamamelididae, Dilleniidae, Liliidae, and Arecidae, while three-celled, or two-plus three-celled, families are most common in the Caryophyllidae, Alismidae, and Commelinidae. A much more detailed analysis of this pollen characteristic has been made by Brewbaker (1967), who presented data for 1908 species from 1219 genera in 265 families. Of these families 179 were entirely binucleate, 54 entirely trinucleate, and 32 both bi- and trinucleate. Many of the largest families, such as the composites, orchids, and grasses, had a single pollen type. He found that "with almost surprising regularity binucleate and trinucleate pollen types are mutually exclusive in angiosperm species and genera. Only 10 genera studied include both binucleate and trinucleate species." Of these 10 genera Brewbaker accepted only 5 as convincingly containing both types of pollen. He arranged the families and the information he had compiled on two family trees, the one for the dicots following Takhtajan (1954) and that for the monocots following Hutchinson (1959). It is recommended that the reader study these informative diagrams in the original paper (Brewbaker, 1967). With the aid of these he was able to draw a number of conclusions about the occurrence of trinucleate pollen. (a). Aquatic taxa with submersed flowers normally have trinucleate pollen (3 genera are exceptions), but this does not apply to emersed flowers of subaquatic or marsh plants. (b). "Trinucleate taxa regularly trace back to binucleate taxa, while the reverse need not be postulated in a single instance. Schüroff's (1926) proposal that trinucleate pollen is a phylogenetically advanced trait appears wholly validated." (Brewbaker, 1967: 1071). (c). Trinucleate pollen has arisen independently many times during angiosperm evolution. In the line of evolution through the Rosales trinucleate pollen appeared many times; for example, there are six "mixed" families in the Gentianales alone. In contrast to this the other major evolutionary lines show a less frequent appearance of the trinucleate condition: once in the Hamamelidales line, once in the Ranales, five in the Theales, and at no more than six sites in the monocotyledons. A number of these sites of origin are related to the evolution of aquatic taxa. (d). "We must conclude that the earliest angiosperms were endowed with a unique binucleate pollen grain, distinguishing them from more primitive taxa." (Brewbaker, 1967: 1082).

The Caryophyllidae is the only subclass of angiosperms in which no family has exclusively anatropous ovules though they do occur in some families in conjunction with other types. The predominant types are the curved ones—campylotropous and amphitropous—alone or in conjunction with others. The larger subclasses Dilleniidae, Rosidae, Asteridae, and Liliidae show predominantly anatropous ovules and this is also true of the smaller Ranunculidae, Alismidae and Arecidae. Of 18 families in which the ovules are exclusively orthotropous, 6 are in the Magnoliidae (Chloranthaceae, Piperaceae, Saururaceae, Rafflesiaceae, Hydnoraceae, Ceratophyllaceae), 3 in the Hamamelididae, and 4 in the Commelinidae. The basic type of ovule would appear to be the anatropous; it occurs in the Magnoliales, Ranunculales and Alismales, and is found in all "central" orders as well as being characteristic of such advanced families as the Asteraceae and Orchidaceae. The other types have probably arisen independently several times and the occurrence of, for example, an orthotropous ovule in two families is not a good indication that these families are related.

As pointed out earlier, unitegmic ovules are almost exclusively a feature of dicotyledons. In general the number of integuments is a family characteristic: of 281 dicotyledonous families only 19 have both unitegmic and bitegmic ovules. The unitegmic condition is thought to be derived from the bitegmic either by fusion of the two or by loss of one; ovules showing intermediate steps in both fusion and loss have been described. The distribution of the two types of ovules among the dicots also indicates that the unitegmic condition is derived. Two integuments are predominant in the Magnoliidae, Ranunculidae, and Caryophyllidae; the proportion of families having a single integument increases slightly in the Hamamelididae and Dilleniidae (here they all occur in one superorder, the Ericanae), while in the Rosidae, families with unitegmic ovules outnumber those with bitegmic ones about 3 to 1, and the Asteridae are almost exclusively unitegmic.

In addition to number of integuments, their thickness in cell layers, commonly at the mature ovule stage, has often been recorded, but one aspect which is rarely described in research papers and has not been covered by Davis (1966) at all is their ontogeny. Bouman (1971) and de Boer & Bouman (1972) have expressed the opinion that characters of seed coats (mature integuments) may be of doubtful taxonomic significance unless accompanied by observations of development, since apparently-similar multilayered integuments may have arisen differently during development. They also suggested that "histogenesis of the integuments must be taken into account in discussions concerning the homology of integuments" (de Boer & Bouman 1972: 627).

The extent of the nucellus beyond the megaspore mother cell has been described for over 300 families. As pointed out earlier, it may be composed of a single layer of cells, and the ovule be tenuinucellate, or there may be one to several layers of cells between the outer layer and the sporogenous tissue. These layers may have been derived from the parietal cell(s) formed by division of the archesporial cell(s) (crassinucellate ovule), by division of the epidermal layer (may be differentiated from the parietal type and called pseudocrassinucellate), or by both. In a little less than two-thirds of the families described all ovules are crassinucellate; a number show some genera crassinucellate and others tenuinucellate. No families characterized by tenuinucellate ovules are found in the Hamamelididae, Caryophyllidae, or Arecidae and only a few occur in the Magnoliidae and Ranunculidae (Rafflesiaceae, Hydnoraceae, Sarraceniaceae, Circaeastraceae, and most of the Podophyllaceae). The Rosidae families are 3 to 1 crassinucellate but the tenuinucellate families occur primarily in the superorders Rosanae and Celastranae; similarly the Dilleniidae are 2 to 1 crassinucellate but again almost all the tenuinucellate families are in one superorder, the Ericanae. Families of the Alismidae and Liliidae are also about 2 to 1 crassinucellate while those of the Commelinidae are about equally divided between crassi- and tenuinucellate. The Asteridae are almost completely tenuinucellate with only some genera of the Convolvulaceae and the *Ehretia* section of the Boraginaceae forming parietal tissue, while the Asclepiadaceae and a rare species in the Lamiaceae show divisions in the nucellus.

Young & Watson (1970), in a computational analysis of 543 genera based on 83 attributes, many of which were embryological, arranged the dicot families considered in two main groups, "Crassinucelli" and "Tenuinucelli," thus emphasizing the possible significance of variation in this ovular character among the angiosperms. Their treatment of families corresponds only in part with the orders and superorders of Cronquist (1968) and Takhtajan (1969).

The amount of tissue built up in crassinucellate ovules varies from very little to considerable. Ovules with thick nucelli are found primarily in the Magnoliidae, the superorders Dillenianae and Malvanae of the Dilleniidae, in about half the families of the Hamamelididae, and in several families of the Rosidae, particularly in the superorder Rutanae. All nucelli in crassinucellate monocots tend to be moderately-thin to thin. Although this is rarely stated in Davis's (1966) synopsis of a family, in the Ericanae and Asteridae the single nucellar layer normally degenerates completely between the tetrad and mature megagametophyte stages so that the latter is in contact with the inner layer of the integument. It is mostly these families that show Swamy & Krishnamurthy's (1970) "true" endothelium.

A comparison of the distribution of unitegmic ovules, the tenuinucellate condition, and an endothelium shows that they frequently, though not invariably, occur together. As stated earlier, unitegmic, tenuinucellate ovules with an endothelium are concentrated in the Asteridae and Ericanae, and are found also in another group of families occurring in the Aralianae of the Rosidae (here some families have ovules with one or occasionally two parietal layers although the Apiaceae are strictly tenuinucellate). This distribution suggests that the tendency to one integument, no build-up of nucellus, and differentiation of an endothelium must have been expressed in two different major evolutionary lines of the dicotyledons, as proposed by Cronquist (1968) and Takhtajan (1969), one through the Rosales to the Scrophulariales, Polemoniales, Lamiales, Asterales, etc. of the Asteridae and to the Aralianae of the Rosidae and the other through the Theales to the Ericanae.

Two integuments so commonly go hand-in-hand with the crassinucellate condition and one integument with the tenuinucellate condition that Philipson (1974) recently advocated that considerably greater emphasis be placed on these aspects of the ovule in determining relationships, and in proposing major phyletic lines, within the dicotyledons. He discussed the distribution of the two characteristics, particularly the exceptions to two integuments occurring with the thick, and one with the thin, nucellus, and attempted to distinguish between what he called "the sporadic independent acquisition of the characters and their consistent presence in major evolutionary lines" (Philipson, 1974: 90). This recommendation would involve removal of the families of the ericalean complex from the Dilleniidae and their alliance with the other sympetalous families of the Asteridae and thus recognize a single major evolutionary line for the sympetalous dicotyledons.

It has already been suggested that the crassinucellate, bitegmic ovule is the primitive one. Support for this conclusion has been supplied by Sporne (1969), who found several highly significant correlations between the crassinucellate condition or the occurrence of two integuments and other dicotyledonous characters, both floral and vegetative, which are correlated and considered to be primitive.

Although 10 different patterns of megagametophyte development are generally accepted and others have been suggested, only one—the *Polygonum* type—is at all common. Maheshwari, in 1950, stated that it occurred in at least 70% of the angiosperms then known. At the present state of knowledge, the *Polygonum* type is the only type of development reported for almost 80% of the families where development has been described (294). Only 11 families are characterized by a different single type of development. In the 56 families showing two or more patterns of development, the *Polygonum* type usually predominates: of the 20 different combinations of types which have been reported to occur in any family, the *Polygonum* type occurs in 16 and is apparently the predominant type in at least 9 of these combinations. Although, from the compiled data, there is no clear information about the total numbers of species involved, the family figures suggest rather strongly that the *Polygonum* type of development is even more prevalent than Maheshwari's 70% or the 80% of the families would indicate. It predominates in all subclasses of the angiosperms with the Rosidae containing more families either with a single different type of development (5 families and 5 different types of development) or a combination of types (16 families). Of the variant patterns of development, the *Allium* type is most frequent, characterizing 6 families and occurring with the *Polygonum* type in 29 families and as one of the types in 10 other combinations. It is an uncommon type in the Magnoliidae and Ranunculidae. The other variants are more restricted in distribution. The *Oenothera* type characterizes the Onagraceae (Rosidae) and apparently does not occur elsewhere. The *Drusa* type, in a reduced version, occurs in all Limnanthaceae (Rosidae) and is found usually in only 1 or 2 species in 7, possibly 9, other families scattered from the Hamamelididae to the Liliidae (Ulmaceae, Euphorbiaceae, Tamaricaceae, Apiaceae, Scrophulariaceae, Asteraceae, and Liliaceae). *Penaea* type development, as would be expected from its name, characterizes the Penaeaceae (Rosidae) and is found elsewhere in some Combretaceae and Malpighiaceae, one species of Apiaceae (all Rosidae), questionably in one species of the Plumbaginaceae (Caryophyllidae) and in a few Euphorbiaceae (Dilleniidae). Development of the *Peperomia* type characterizes the Gunneraceae (Rosidae), has been reported to occur in modified form in one species of Berberidaceae (Ranunculidae), is typical of *Peperomia* of the Piperaceae (Magnoliidae), is found in two species of Rubiaceae and possibly in some Asteraceae (listed in the Delhi seminar synopsis but not Davis) (Asteridae), and is reported for one species of the Euphorbiaceae (Dilleniidae). The *Adoxa* type characterizes the Adoxaceae (Asteridae) and elsewhere has been found to occur occasionally in one genus of Hydnoraceae (Magnoliidae), in some ovules of the Ulmaceae (Hamamelididae), in one species of the Aizoaceae and occasionally in two genera of Plumbaginaceae (Caryophyllidae), in one species of the Euphorbiaceae (Dilleniidae), in two species of Solanaceae, the genus *Sambucus* of the Caprifoliaceae, and one species of Asteraceae (Asteridae), in four genera of Liliaceae, one species of Trilliaceae and of Zingiberaceae, and occasionally in some Orchidaceae (Liliidae), and in one species of Commelinaceae and five of the Poaceae (Commelinidae). None of the other three variants—*Fritillaria, Plumbago* and *Plumbagella*—is characteristic of an entire family. The latter two occur only in the Plumbaginaceae, the *Plumbago* type in two genera and the *Plumbagella* type in one. The *Fritillaria* type of development, which more people have probably seen than any other (even the *Polygonum* type), since it occurs in *Lilium* and *Fritillaria,* the only genera for which slides showing megagametophyte development are sold commercially, occurs in a wider range of families: in two genera of the Piperaceae (Magnoliidae), two genera of the Plumbaginaceae (Caryophyllidae), irregularly in one species and occasionally in others of the Tamaricaceae and in one species of the Euphorbiaceae (Dilleniidae), in one species of Cornaceae (Rosidae), in some of the Asteraceae (Asteridae), and in five genera of the Liliaceae (Liliidae).

While a single type of megagametophyte development occurs in the majority of families, there are, as has just been pointed out, a number of families in which more than one type has been found. Mixed families occur in all subclasses of angiosperms but are less frequent in the Magnoliidae, Ranunculidae, Hamamelididae and Alismidae, and more common in the Asteridae and Liliidae. In the mixed families a particular type of development often characterizes a genus, but there are a number of examples where different species of a single genus develop via different pathways, and variation also may occur within a single species, even within the same inflorescence or the same individual. Variation within species has been reviewed by Hjelmqvist (1964). The families showing the greatest intrafamilial variation are the Euphorbiaceae, Plumbaginaceae, Asteraceae, and Liliaceae, all showing five or six different types of development.

The commonly held opinion is that the monosporic 8-nucleate gametophyte (*Polygonum* type) is the most primitive. As pointed out by Maheshwari (1950), it is rather easy to conceive of all variants being derived from the *Polygonum* type by failure of walls to form after meiosis II or after both meiosis I and II and by a reduction in the number of mitoses. A change in the reverse direction—from any of the different types to the *Polygonum* type—is much more difficult to envision. Such a change would involve an addition of walls (as in the tetrad) and an increase in number of mitoses (no variant has more than two mitoses while the *Polygonum* type has three), and the general tendency throughout the vascular plants has been toward a reduction in the gametophyte, not an increase. Within many of the types of angiosperm megagametophyte development, there has been additional evidence of reduction in mitoses. While the nucleus at the micropylar end of the developing megagametophyte always completes all divisions, one or more of those toward the chalazal end may not divide. In certain basically bisporic and tetrasporic megagametophytes this failure of divisions at the chalazal end has gone so far as to make the gametophyte pseudomonosporic, as in the Podostemaceae (*Allium* type), Limnanthaceae (*Drusa* type), and three species of Asteraceae (*Drusa* type). Anyone who has looked at a number of examples of the final stages of megagametophyte development in lily may well have seen an example of this reduction in mitoses. The chalazal-most nucleus of the 4-nucleate megagametophyte may often divide aberrantly, giving rise to two partially degenerated nuclei, or it may degenerate without dividing, so that the mature gametophyte has only one "normal" antipodal cell. Because of the widely scattered distribution of certain of the different types, it would appear that they had arisen independently in several families.

In spite of differences in pattern of development, the basic organization of the mature megagametophyte is amazingly constant, and it is in most cases not possible to determine the type of developmental pattern by observation of the mature structure. *Polygonum*, *Allium*, *Fritillaria* and *Adoxa* types of development all give rise to a similar gametophyte, and if one remembers that the antipodal cells are often ephemeral in any of these types and are commonly so in the *Drusa* type, and also remembers that the polar nuclei usually fuse, it then becomes impossible to be sure whether development follows one of the first four, the *Drusa*, or the *Oenothera* pattern without seeing the critical developmental stages.

The initiation of endosperm by a second fertilization—the fusion of the second male gamete with the polar nuclei—is a constant feature of normal sexual reproduction in angiosperms and serves to distinguish them from all other plant taxa. The chromosome number of the endosperm nuclei is not constant, however. Because of the origin of the endosperm from the polar nuclei of the megagametophyte plus one $1n$ male nucleus, its ploidy varies with the number and ploidy of the polar nuclei and is thus related directly to the type of megagametophyte development. Endosperm is most commonly $3n$ since two $1n$ polar nuclei are found in gametophytes of the *Polygonum*, *Allium*, *Drusa*, and *Adoxa* types. It will be $2n$ in *Oenothera* type gametophytes where there is a single $1n$ polar nucleus. It is $5n$ in gametophytes of the *Penaea* and *Plumbago* types where there are four $1n$ polar nuclei and also in the *Fritillaria* and *Plumbagella* types in which there are only two polar nuclei but one is $3n$ and the other $1n$. The ploidy may be 8, 9 or $15n$ in different variations of the *Peperomia* type, the $15n$ occurring in *Peperomia hispidula* in which the megagametophyte has 1 synergid, 1 egg, 14 polar nuclei and 0 antipodal cells.

As was shown earlier, development of the endosperm may follow one of three patterns, and cellular endosperm is primarily a characteristic of the dicots and helobial of the monocots; in both classes other families have a nuclear type of development. Within the Liliatae and Magnoliatae cellular and helobial endosperm are not distributed evenly throughout the different subclasses. Among the monocots, helobial endosperm is most characteristic of the Alismidae (includes the old Helobiales from which the type takes its name), frequent in the Liliidae, and is not found in any family of the Arecidae. It is in the latter subclass that the only two monocot families with a cellular endosperm development—the Araceae and Lemnaceae—are placed. Among the dicots, a preponderance of families in the Magnoliidae and Asteridae have a cellular endosperm development. Within the Dilleniidae and Rosidae where the endosperm of a fair number of families is cellular, distribution is again concentrated in certain areas—in the Ericanae of the Dilleniidae and in the Rosanae (particularly the Saxifragales), Aralianae, and Celastranae (primarily among the Santalales) of the Rosidae. Several families of the Ranunculidae also have a cellular endosperm only: Schisandraceae, Lardizabalaceae, Circaeastraceae, Sarraceniaceae, and perhaps also the Illiciaceae (Davis lists only cellular, but the Delhi seminar synopsis lists both cellular and nuclear). Thus it can be seen that cellular endosperm might be said to have a bimodal distribution, occurring in several primitive families (Magnoliidae and Ranunculidae) and a larger number of derived families (Asteridae, Ericanae, Aralianae, Santalales) and only occasionally in more central families (Saxifragales). The cellular endosperm of the derived families frequently gives rise to haustoria, often both micropylar and chalazal; that of the primitive families only occasionally exhibits an haustorium; more commonly it does not. The "advanced" cellular endosperm, with haustoria, commonly develops in the unitegmic, tenuinucellate ovules with an ephemeral nucellus and an endothelium which were discussed earlier.

Two divergent views have been expressed as to the direction of evolution of the endosperm. Some have held that nuclear development is primitive and others that cellular is the original type. In this connection Cronquist (1968) pointed out that it seems clear that in the Gentianaceae nuclear endosperm, characteristic of most of the family, is primitive and the cellular development found in *Voyria* and *Voyriella* is advanced. These genera lack chlorophyll and show other specialized features. He thought it unlikely that such specialized genera would have retained a primitive character (if cellular endosperm were primitive) that had been lost in the rest of the family. What is true for one family need not be true for the angiosperms as a whole, however. Sporne (1954) found nuclear endosperm development in dicotyledons to be statistically correlated with a variety of floral and vegetative characters: woody habit, secretory cells in leaves, stipules present, stamens pleiomerous, ovules with two integuments, and integuments with vascular bundles. He had earlier shown these characteristics to be part of a broader character-correlation which he interpreted as primitive. Accordingly, he concluded that nuclear endosperm should also be considered primitive. This conclusion was criticized by Swamy & Ganapathy (1957). Sporne (1967) conducted further statistical analyses including, among other new characters, features of the xylem. Four xylem characters were highly correlated and are generally accepted as primitive. Nuclear endosperm correlated negatively with two of these. Taken alone these negative correlations would suggest that nuclear endosperm was advanced. Sporne pointed out, however, that nuclear endosperm was positively correlated with ten characters (adding leaves alternate, petals free, and seeds arillate to the list above) which themselves were positively correlated (often with a very much higher positive correlation than the two negative ones) with primitive xylem. Nuclear endosperm was still suggested as primitive but the two negative correlations remained unexplained.

Lowe (1961) statistically analyzed a considerable number of floral characteristics of monocotyledons and found 17 of them to be positively correlated and primitive for that class. Among the 17 characters six were embryological: pollen development simultaneous, megagametophyte monosporic, parietal cell formed, anatropous ovule, binucleate pollen, and endosperm cellular or helobial—the latter in direct contrast to Sporne's suggestion that nuclear endosperm is primitive in the dicots. If one accepts that monocots were derived from early dicot-like ancestors, it is difficult to accept a different type of endosperm development as being primitive in the two lines. Probably the strongest proponent for the cellular type of development being the primitive one is Wunderlich (1959). She gave data for all families known and compared endosperm development with ovule type throughout the angiosperms. Her analysis showed that crassinucellate ovules usually showed nuclear development and tenuinucellate ovules cellular. Certain families contradicted this relationship, particularly the "Polycarpicae." She felt that the original angiosperms possessed a crassinucellate, bitegmic ovule and cellular endosperm. During evolution of the ovule and endosperm, if the nucellus remained large or increased in size, as is the case in primitive families, space relations favored the appearance of nuclear endosperm; thus nuclear endosperm appeared early in the evolution of angiosperms. Where the nucellus decreased in size and became tenuinucellate, the condition characterizing advanced families, development of the endosperm was inhibited because of the decreased space and endosperm development remained cellular.

Other variations among embryological characteristics could be related to the major angiosperm taxa, but those already discussed will suffice to show the extent to which embryology correlates with a natural classification. A few characters show a moderately clear segregation among the classes or subclasses, but others are rather evenly distributed throughout.

EMBRYOLOGY AT THE FAMILY AND LOWER TAXA LEVEL

It should have become clear in the course of the preceding discussions that embryological characteristics are much more constant for the family than for taxa at the higher levels. For all characteristics some families are variable and in these the genus is commonly constant. It is at approximately the level of the family that embryological characters have most frequently been used to supplement others in arriving at taxonomic conclusions; sometimes families within an order have been considered, sometimes tribes of a family, sometimes individual genera. A few examples will be mentioned briefly. Details of these and of additional cases can be found in papers by Maheshwari (1950, 1956, 1961, 1963a), Cave (1953), Kapil (1962), Johri (1963, 1967), and Bhojwani & Bhatnagar (1974).

Occasionally a single characteristic is particularly distinctive, as in the case of the Podostemaceae. In this famly no endosperm develops and a "pseudo-embryo sac," formed by the disintegration of nucellar cells immediately below the megagametophyte, apparently takes over the functions of the endosperm. This is unmatched in any other family. Another family recognizable by one individual characteristic is the Onagraceae. This is the only family with an *Oenothera* type of megagametophyte development and that type of development has been found in every member of the family studied. The removal of *Trapa* from the Onagraceae, where it had tentatively been placed by various authors, is strongly supported by its possession of a *Polygonum* type of development. The Cyperaceae is another family with a distinctive characteristic: its pollen grain. After the formation of the four microspore nuclei, three of them are cut off to one side of the pollen grain and only the fourth divides to form the tube and generative cells and then the two sperms. This "pseudomonad" or "cryptotetrad" is found in all Cyperaceae and elsewhere only in some of the Epacridaceae in which, besides other differences, the mature pollen is two- not three-celled. In all three families, although a single characteristic has been stressed, it occurs in combination with others which serve to characterize the family.

In other cases no single feature is by itself distinctive but a particular combination of characteristics occurs together so regularly as to be considered diagnostic. There are instances of this sort where embryological data have been used to support or suggest the removal of a genus (or group of genera) from one family into a new one of its own. Examples are the Butomaceae and Limnocharitaceae, Menyanthaceae and Gentianaceae, Sphenocleaceae and Campanulaceae, etc.

Such constellations of characters have played a role in rearrangements of genera among the various liliaceous subfamilies and tribes, and have strongly supported the classification of the Lemnaceae in the Arales rather than in the Alismales.

The taxon which I know best is an excellent example of the use of embryology for taxonomic purposes. Samuelsson (1913) recognized early that the Ericales were characterized by a distinctive battery of embryological characteristics. To the list already published (Maheshwari, 1950; Palser, 1961) can be added embryo development of the Solanad type (Johansen's system) or belonging to the 9th or 11th group (2nd period, megarchetype III; Souèges's system) since Veillet-Bartoszewska (1963) has followed embryogeny in several species. No one characteristic by itself can be considered diagnostic, and many of them are those prevalent among the dicots or at least among the sympetalous ones. A few of the features are less widely distributed: permanent tetrads, absence of a differentiated endothecium in the anther, shape of the mature megagametophyte, and the linear arrangement of the first four cells of the endosperm. The entire group of characters taken together, however, does not occur elsewhere among the angiosperms. Samuelsson first recognized this embryological syndrome on the basis of his own observations, supplemented by earlier ones, dealing with roughly 30 species. Study of many more species since that time, while turning up a few exceptions, has served primarily to add considerable support to the consistency with which this constellation of characteristics occurs in the order.

The mutual relationship among the Ericaceae, Epacridaceae, Pyrolaceae, Clethraceae, and also Vacciniaceae and Monotropaceae if they are segregated from the others, has long been recognized. Several small families have, at one time or another, been included with the central ones in the Ericales: Empetraceae, Lennoaceae, Diapensiaceae, Cyrillaceae, Grubbiaceae, and most recently (Takhtajan, 1969) the Saurauiaceae and Actinidiaceae. Samuelsson (1913) was the first to point out that the Empetraceae had ericalean embryology, and a recent paper (Vijayaraghavan, 1969) on one species of the Cyrillaceae lends support to the inclusion of this family in the order. What details are known of the embryology of the Actinidiaceae-Saurauiaceae (Schnarf, 1924; Souèges, 1943; Crété, 1944; Vijayaraghavan, 1965) and Grubbiaceae (Fagerlind, 1947; Johri & Bhatnagar, 1960) are not inconsistent with their inclusion in the Ericales (Takhtajan, 1969), although Cronquist (1968) retained the Actinidiaceae-Saurauiaceae in the Theales and the Grubbiaceae in the Santalales. On the other hand, what little embryological data there are for the Lennoaceae (Copeland, 1935) do not fit well with the ericalean characters and the family is now normally classed in the Polemoniales. All these families could well stand observation of more embryological details and additional species. The Diapensiaceae are better known (Samuelsson, 1913; Palser, 1963; Veillet-Bartoszewska, 1963; Yamazaki, 1966; Reynolds, 1968). They agree with the Ericales in those characters that are widely distributed such as two-celled pollen; unitegmic, tenuinucellate, anatropous ovule; *Polygonum* type of megagametophyte development formed from the chalazal spore of the tetrad; and cellular endosperm. They differ in a few of the common and all of the more unusual aspects: pollen is not in tetrads; an endothecium is differentiated; there is no endothelium although the nucellus doe disintegrate; the megagametophyte is oval rather than showing an enlarged micropylar end; the first four cells of the endosperm are rarely linear; there are no endosperm haustoria; and embryogeny, while classed as Solanad by Johansen's system, is distinct (3rd group, 1st period, megarchetype IV; Souèges's system). In addition, there are other differences in anther development and structure, etc. Accordingly, the family has been removed from the Ericales and assigned to an order of its own which, at least for the present, is retained close to the Ericales (Cronquist, 1968; Takhtajan, 1969).

All characteristics discussed so far have been major developmental patterns, and the smaller differences, such as the size and shape of the ovule or of the developing or mature megagametophyte, characteristics of individual cells (for example, the synergids or antipodals), the arrangement of the early cells of the cellular endosperm and origin of the associated haustoria, etc. have been disregarded. These characteristics show a great deal of variation, however, and might well prove useful for helping to determine relationships within families or genera, particularly where the grosser characteristics are consistent throughout the taxon. In this regard, Cave (1953: 140) has stated that "variation in the gametophyte generation would seem to be as important in the study of phylogeny of genera as changes in the sporophyte generation. Because of the extremely reduced nature of the angiosperm gametophyte, small variations have great significance in tracing relationships." The significance of variation in, for example, the *Polygonum* type of megagametophyte development was pointed out by Herr (1967), who wrote: "small alterations in the developmental pattern constitute variations of high magnitude in the light of extremely low levels of structural complexity." He was of the opinion that more attention to detail would probably result in more comprehensive delimitation of generic, specific, and even individual distinctions in the megagametophyte of angiosperms. This generalization was followed (Smith & Herr, 1971) by a quantitative analysis, for one species, of development of the ovule from initiation to early embryogeny. This led to the conclusion that the size of the developing megagametophyte merits attention and "should be accorded special attention in studies designed to clarify phylogenetic relationships on the basis of megagametophyte structure."

Data for this detailed sort of analysis have not been accumulated, as they have been for the grosser characteristics and, moreover, are frequently not available. The only light that I can throw on this subject comes from some of my own comparative studies within the Ericaceae. Megagametophyte development has been followed for several species in each of two tribes, the Andromedeae (Palser, 1952) and the Phyllodoceae (Ganapathy & Palser, 1964). Comparisons were at a general, not quantitative, level. Mature ovules and megagametophytes are diagrammed at the same magnification in the two papers. Some differences could be detected among the several genera of the Phyllodoceae, while in the Andromedeae several rather striking differences in ovule size and shape, megagametophyte size and shape, and/or cellular characteristics were apparent. These were correlated with individual genera or groups of genera and tied in remarkably well with proposed taxonomic relations within the tribe. These tribes afford evidence that details can be useful in emphasizing the presence or absence of homogeneity within a group of supposedly closely related genera or in suggesting possible relationships among individuals within a larger taxon.

Although in the studies of Andromedeae and Phyllodoceae two or more species of several of the genera were observed, the comparisons are primarily of interest at the generic level. The question then arises, can a similar type of analysis be useful among species of a single genus? At the present time I am engaged, with W. R. and M. N. Philipson of New Zealand, in a comparison of the ovule and megagametophyte throughout the very large genus *Rhododendron.* This genus seems an appropriate one for this type of study. Not only does it show a great deal of gross variation but, because of its horticultural interest, it has received extensive study from the taxonomic point of view. Thus, any ovule variations found can be related to a rather well established intrageneric classification of species. Only one paper has been published (Palser et al., 1971) so far; this treats development of a single species in detail. Records of observations of over 125 species, giving essentially complete coverage of all subcategories recognized in the genus, are gradually accumulating. Since some of these records are in this country and others in New Zealand and the information contained has not yet been synthesized, what the outcome will be is not known. Differences definitely do exist, but whether these will show any correlation with taxonomic subdivisions of the genus remains to be seen.

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NOTE ADDED IN PROOF

Since this paper went to press, a discussion of the distribution among angiosperms of four of the embryological characteristics presented in some detail in the section starting on p. 633—bitegmic versus unitegmic ovules, crassinucellate versus tenuinucellate ovules, cellular and helobial versus nuclear endosperm development, and binucleate versus trinucleate pollen—has been published (Dahlgren, 1975). The author concluded that the condition given last above for each of the four characteristics is most probably the secondary state. The reader is referred to this paper for details not incorporated in the present article and for very informative diagrams.

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